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Spatially Inhomogeneous Steady State Solutions for Systems of Equations Describing Interacting Populations

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1. INTRODUCTION

The system of reaction diffusion equations

$$\begin{aligned} u_t(x, t) &= d_1\, \Delta u(x, t) + au + uf(u, v), \\ v_t(x, t) &= d_2\, \Delta v(x, t) + bv + vg(u, v) \end{aligned} \tag{1.1}$$

for $x \in \Omega$ and $t \geqslant 0$, where Ω is a bounded region in R^n ($n = 1, 2, 3$) and Δ denotes the Laplacian, models the interaction of two species co-existing in Ω; the densities of the species at time t and at the point $x \in \Omega$ are given by $u(x, t)$ and $v(x, t)$. The constants $d_1, d_2 > 0$ give the rates at which the species diffuse. The constants a and b give, if positive, the birth rates and, if negative, the mortality rates of the species. So that system (1.1) has a unique solution we must specify initial conditions, i.e., $u(x, 0)$ and $v(x, 0)$, and boundary conditions. We shall be interested in the case of Dirichlet boundary conditions, i.e., in the case where $u(x, t)$ and $v(x, t)$ are specified functions of x on $\partial\Omega$.

Co-existing populations may interact in various ways, e.g., they may compete or co-operate with each other or one may be a predator preying on the other. The nature of the interaction is reflected by the properties of the terms $f(u, v)$ and $g(u, v)$. For example, if the v population preys on the u population, an increase in v would lead to a decrease in u and so it would be natural to assume that $\partial f/\partial v < 0$. Throughout we shall assume that

$$f(0, 0) = g(0, 0) = 0 \tag{1.2}$$

and that

$$\frac{\partial f}{\partial u}(u, v) < 0 \qquad \text{and} \qquad \frac{\partial g}{\partial v}(u, v) < 0 \qquad \text{for all} \quad u, v \geqslant 0 \tag{1.3}$$

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and that for each $k \geqslant 0$ there exist u_k, v_k such that

$$a + f(u, k) < 0 \qquad \text{for} \quad u \geqslant u_k \tag{1.4}$$

and

$$b + g(k, v) < 0 \qquad \text{for} \quad v \geqslant v_k.$$

Assumptions (1.2) and (1.3) model the fact that the populations are self limiting, i.e., ignoring diffusion effects one of the populations would not grow without limit were the other population absent.

In this paper we investigate the existence of multiple spatially inhomogeneous steady state solutions of (1.1) in the case where v equals a specified non-negative function and u equals 0 on $\partial\Omega$. Thus we are interested in solutions of

$$\begin{aligned} -d_1 \Delta u &= au + f(u, v)u && \text{for} \quad x \in \Omega, \\ -d_2 \Delta v &= bv + g(u, v)v && \text{for} \quad x \in \Omega; \\ u(x) = 0 \text{ and } v(x) &= \phi(x) \geqslant 0 && \text{for} \quad x \in \partial\Omega. \end{aligned} \tag{1.5}$$

We shall assume that Ω has smooth boundary, that f, g and ϕ are all smooth functions and that ϕ is not identically zero.

Two main approaches have been used in the literature to prove the existence of solutions of systems like (1.5). The existence of one steady state solution for (1.5) could be proved by studying the corresponding parabolic system as described in Amann [1] or by using degree theoretic methods as described in Hadeler *et al.* [6] and Tsai [12]; the fact that the system is self limiting is precisely what is required in order to apply the theorems in the above works. There does not seem, however, to be any obvious way to prove the existence of multiple solutions by using these degree theory techniques. Many examples can be found in the literature where the existence of multiple solutions is proved by showing that bifurcation occurs from an obvious spatially constant steady state solution (see, e.g., Auchmuty and Nicolis [3], Herschkowitz-Kaufman [7], Catalano *et al.* [4]). As we show in Section 2, there is an obvious steady state solution, viz., when $u \equiv 0$; however, the v component of this solution is spatially inhomogeneous and although a bifurcation analysis of (1.5) about this obvious solution is possible and yields some results, such an analysis does not seem to be the most fruitful line of attack.

Our approach in this paper is to decouple the equations. We first fix u and show that the second equation in (1.5) has a unique solution $v(u)$; we then substitute $v(u)$ into the first equation of (1.5) and obtain an equation for u which we treat as a bifurcation problem. A similar decoupling technique was used by Rothe in [11] on a system related to the Fitzhugh–Nagumo equation; in that case, however, the system is more weakly coupled than (1.5) and is linear in one of the unknown variables.

Equation (1.5) has been studied by Leung and Clark in [8] in the case of predator–prey systems. In [8] sub- and supersolution techniques are used to prove the existence of multiple steady state solutions of (1.5); the results obtained in [8] suggest that bifurcation occurs and motivated the present investigation. For this case we can give a precise description of where bifurcation occurs and are able to prove the existence of multiple solutions for large ranges of parameter values. Our results are also linked to recent work of Pao in [9] where sub- and supersolution techniques are used to study Eq. (1.5) with various homogeneous boundary conditions in the case of competing populations.

Our results agree with what one would expect of the systems modelled by the equations. The inhomogeneous boundary condition satisfied by v ensures that v is being constantly supplied to the system. If the birth rate a of the u population is very low (or perhaps if the mortality rate is high) then we would expect v to swamp u so that all possible steady state solutions will have $u \not\equiv 0$. If, however, the birth rate of u is sufficiently large one would expect u to be able to co-exist with v and so steady state solutions with $u \not\equiv 0$ should exist. Moreover, a higher u birth rate should be necessary for co-existence if v preys on u than if the presence of v encourages the growth of u. Our results give precise expression to all these expectations.

In the remainder of this section we discuss some preliminaries which are required later in the paper. In Section 2 we show how the equations may be decoupled and in Section 3 we analyze the resulting bifurcation problem for various types of systems.

Since u and v represent population densities, we are interested only in solutions such that $u \geqslant 0$, $v \geqslant 0$. Thus we may regard the functions f and g as being defined initially only on $R^+ \times R^+$; for convenience we extend their domain of definition to $R \times R$ by defining $f(u, v) = f(\max\{u, 0\}, \max\{v, 0\})$ and similarly for g. The functions thus defined are Lipschitz continuous.

The criteria we derive for the existence of multiple solutions are expressed in terms of the least eigenvalues of certain boundary value problems. We now introduce a convenient notation for such eigenvalues. Let q be any smooth function and consider the eigenvalue problem

$$-d_1 \Delta w - qw = \lambda w \quad \text{for } x \in \Omega; \qquad w(x) = 0 \quad \text{for } x \in \partial\Omega. \tag{1.6}$$

It is well known that (1.6) has an infinite sequence of eigenvalues which is bounded below. We shall denote the least eigenvalue by $\lambda_1(q)$. It is well known that $\lambda_1(q)$ is a simple eigenvalue and that the corresponding eigenfunctions do not change sign on Ω.

We shall find it convenient for the most part to work with the function space $C^1(\bar{\Omega})$—the space of functions which are continuously differentiable on $\bar{\Omega}$; we shall use the symbol $\| \ \|$ to denote the usual $C^1(\bar{\Omega})$ norm.

2. Decoupling the Equations

We assume that f and g satisfy (1.2), (1.3) and (1.4) and in addition that g is a monotone function of u, i.e., that either

$$\frac{\partial g}{\partial u}(u, v) > 0 \qquad \text{for all} \quad u, v \geqslant 0 \tag{2.1}$$

or

$$\frac{\partial g}{\partial v}(u, v) < 0 \qquad \text{for all} \quad u, v \geqslant 0.$$

We choose and fix $u \in C^1(\bar{\Omega})$ and then consider the single nonlinear boundary value problem

$$\begin{aligned} -d_2 \Delta v &= bv + g(u, v)v \qquad && \text{for} \quad x \in \Omega; \\ v(x) &= \phi(x) \geqslant 0 && \text{for} \quad x \in \partial\Omega. \end{aligned} \tag{2.2}$$

Theorem 2.1. (i) *Equations* (2.2) *possesses a unique non-negative solution* $v(u)$.

(ii) *The mapping* $u \to v(u)$ *from* $C^1(\bar{\Omega})$ *to* $C^1(\bar{\Omega})$ *is continuous.*

Proof. (i) For fixed u, hypothesis (1.4) allows us to choose $K > 0$ so that $b + g(u(x), K) < 0$ for all $x \in \Omega$. Moreover K can be chosen such that we also have $K > \phi(x)$ for all $x \in \partial\Omega$. Then (2.2) has supersolution $v \equiv K$ and a subsolution $v \equiv 0$ and so has at least one solution lying between 0 and K; in fact it can be shown (see Amann [2]) that there exists a minimal non-negative solution v.

We now show that this solution is unique. Let V be any other non-negative solution of (2.2). Then $V(x) \geqslant v(x)$ for all $x \in \Omega$ and so $(\partial V/\partial n)(x) \leqslant (\partial v/\partial n)(x)$ for all $x \in \partial\Omega$, where $\partial/\partial n$ denotes differentiation in the direction of the unit outward normal to $\partial\Omega$. Thus we have

$$d_2 \int_\Omega (\Delta v \cdot V - v \cdot \Delta V)\, dx = d_2 \int_{\partial\Omega} \left(\frac{\partial v}{\partial n} - \frac{\partial V}{\partial n}\right) \phi\, dx \geqslant 0$$

But, because of hypothesis (1.3), we must also have

$$d_2 \int_\Omega (\Delta v \cdot V - v\, \Delta V)\, dx = \int_\Omega vV(g(u, V) - g(u, v))\, dx \leqslant 0.$$

Hence we must have $\int_\Omega vV(g(u, V) - g(u, v))\,dx = 0$ and so $v = V$. Thus Eq. (2.2) possesses a unique solution which we may denote by $v(u)$.

(ii) Suppose that $\{u_n\}$ is a sequence of functions converging to u in $C^1(\bar{\Omega})$. In order to show that $u \to v(u)$ is continuous it suffices to show that $\lim_{n\to\infty} v(u_n) = v(u)$ in $C^1(\bar{\Omega})$. First we show that $\{v(u_n)\}$ is uniformly bounded in $C^{2+\alpha}(\bar{\Omega})$. Since there exists $M > 0$ such that $|u_n(x)| \leqslant M$ for all n and all $x \in \Omega$, we can find $K > 0$ such that $b + g(u_n(x), K) < 0$ for all n and x and $K > \phi(x)$ for all $x \in \partial\Omega$. Then $v \equiv K$ is a supersolution for

$$\begin{aligned} -d_2\,\Delta v &= bv + g(u_n, v)v && \text{for} \quad x \in \Omega; \\ v(x) &= \phi(x) && \text{for} \quad x \in \partial\Omega \end{aligned} \tag{2.3}$$

and so $0 \leqslant v(u_n) \leqslant K$ for all n. Hence, $bv(u_n) + g(u_n, v(u_n))\,v(u_n)$ is uniformly bounded in $L^p(\Omega)$ for any given $p \geqslant 1$. Thus standard bootstrapping arguments applied to Eq. (2.3) show that $\{v(u_n)\}$ is uniformly bounded in $C^{2+\alpha}(\bar{\Omega})$.

Assume now that $\{v(u_n)\}$ does not converge to $v(u)$ in $C^1(\bar{\Omega})$; we shall obtain a contradiction. We can find a subsequence of $\{v(u_n)\}$ which lies outside a certain C^1-neighbourhood of $v(u)$; this subsequence is uniformly bounded in $C^{2+\alpha}(\bar{\Omega})$ and so possesses a subsequence which converges in $C^2(\bar{\Omega})$ to w say. (For convenience we denote this latter subsequence also by $\{v(u_n)\}$.) Clearly $w \neq v(u)$. Since

$$-\Delta v(u_n) = bv(u_n) + g(u_n, v(u_n))\,v(u_n) \qquad \text{for} \quad x \in \Omega$$

it follows that

$$-\Delta w = bw + g(u, w)w \qquad \text{for} \quad x \in \Omega.$$

Since Eq. (2.2) has a unique solution, it follows that $w = v(u)$. This is a contradiction and so the proof is complete.

The next results illustrate the monotone dependence of $v(u)$ on u.

THEOREM 2.2. *Suppose that* $(\partial g/\partial u)(u, v) > 0$ *for all* $u, v \geqslant 0$. *Then* $v(u) \geqslant v(0)$ *for all* $u \geqslant 0$.

Proof. Choose and fix $u \geqslant 0$. As we saw in the proof of Theorem 2.1, there exists a constant $K > 0$ such that $v \equiv K$ is a supersolution of

$$\begin{aligned} -d_2\,\Delta v &= bv + g(u, v)v && \text{for} \quad x \in \Omega; \\ v(x) &= \phi(x) && \text{for} \quad x \in \partial\Omega. \end{aligned}$$

Clearly $v \equiv K$ is also a supersolution of

$$\begin{aligned} -d_2 \Delta v &= bv + g(0, v) && \text{for} \quad x \in \Omega; \\ v(x) &= \phi(x) && \text{for} \quad x \in \partial\Omega. \end{aligned}$$

Therefore $0 \leqslant v(0), v(u) \leqslant K$. We can now choose a constant $M > 0$ such that $v \to bv + g(0, v) + Mv$ $(=h(v))$ and $v \to bv + g(u, v)v + Mv$ $(=H(x, v))$ are both increasing functions of v for $0 \leqslant v \leqslant K$. Clearly, for fixed v, $h(v) \leqslant H(x, v)$ for all $x \in \Omega$.

It is well known (see Amann [1]) that $v(0) = \lim_{n \to \infty} v_n$, where $v_0 \equiv 0$ and

$$\begin{aligned} -d_2 \Delta v_{n+1} + Mv_{n+1} &= h(v_n) && \text{for} \quad x \in \Omega; \\ v_{n+1}(x) &= \phi(x) && \text{for} \quad x \in \partial\Omega, \end{aligned}$$

and that $v(u) = \lim_{n \to \infty} V_n$, where $V_0 \equiv 0$ and

$$\begin{aligned} -d_2 \Delta V_{n+1} + MV_{n+1} &= H(x, V_n) && \text{for} \quad x \in \Omega; \\ V_{n+1}(x) &= \phi(x) && \text{for} \quad x \in \partial\Omega. \end{aligned}$$

Suppose that $V_k(x) \geqslant v_k(x)$ for all $x \in \Omega$. Then for all $x \in \Omega$

$$\begin{aligned} (-d_2 \Delta + M)(V_{k+1} - v_{k+1}) &= H(x, V_k(x)) - h(v_k(x)) \\ &\geqslant H(x, v_k(x)) - h(v_k(x)) \geqslant 0. \end{aligned}$$

Since $V_{k+1}(x) = v_{k+1}(x)$ for $x \in \partial\Omega$, it follows from the maximum principle that $V_{k+1}(x) \geqslant v_{k+1}(x)$ for all $x \in \Omega$. Thus, as $V_0 = v_0$, it follows that $V_n \geqslant v_n$ for all n. Therefore letting $n \to \infty$ shows that $v(u) \geqslant v(0)$.

COROLLARY 2.3. *Suppose* $(\partial g/\partial u)(u, v) < 0$ *for all* $u, v \geqslant 0$. *Then* $v(u) \leqslant v(0)$ *for all* $u \geqslant 0$.

It is easy to see that (u, v) is a solution of (1.5) if and only if $v = v(u)$ and u is a solution of

$$\begin{aligned} -d_1 \Delta u &= au + f(u, v(u))u && \text{for} \quad x \in \Omega; \\ u(x) &= 0 && \text{for} \quad x \in \partial\Omega. \end{aligned} \tag{2.4}$$

Clearly $u \equiv 0$ is a solution of (2.4) and so $(0, v(0))$ is a solution of (1.5) for all values of a; we shall refer to this solution as the trivial solution. We shall treat a as a bifurcation parameter and regard all the other parameters of the problem, viz., d_1, d_2, b and ϕ, as fixed. By carrying out a bifurcation analysis of (2.4) we shall prove the existence of multiple solutions to (2.4) and so to (1.5).

Equation (2.4) may be written as

$$-d_1 \Delta u - f(0, v(0))u = au + [f(u, v(u)) - f(0, v(0))]u \qquad \text{for} \quad x \in \Omega. \tag{2.5}$$

Let L be the differential expression defined by

$$Lu = -d_1 \Delta u - f(0, v(0))u$$

and consider the eigenvalue problem

$$Lu(x) = \lambda u(x) \text{ for } x \in \Omega; \qquad u(x) = 0 \text{ for } x \in \partial\Omega. \tag{2.6}$$

Using the notation introduced at the end of Section 1, we denote the least eigenvalue of (2.6) by $\lambda_1[f(0, v(0))]$; we denote the corresponding positive eigenfunction by ψ_1. We assume, without loss of generality, that $\lambda_1[f(0, v(0))] \neq 0$, i.e., that L is invertible. (Otherwise we replace L by $L + c$ so that $L + c$ is invertible and write (2.5) as

$$(L + c)u = \tilde{a}u + [f(u, v(u)) - f(0, v(0))]u \qquad \text{for} \quad x \in \Omega,$$

where $\tilde{a} = a + c$, and then argue as below.) Then it is well known that the equation

$$Lu = f \text{ for } x \in \Omega; \qquad u(x) = 0 \text{ for } x \in \partial\Omega$$

has a unique solution for all $f \in L^2(\Omega)$; if we denote this unique solution by Kf, then $K: L_2(\Omega) \to L_2(\Omega)$ (and $K: C^\alpha(\bar{\Omega}) \to C^1(\bar{\Omega})$) is a compact linear operator.

Let $F: C^1(\bar{\Omega}) \to C^\alpha(\bar{\Omega})$ be defined by

$$F(u) = [f(u, v(u)) - f(0, v(0))]u.$$

Then F is continuous and using Theorem 2.1(ii) we see that $\|F(u)\|_\alpha = o(\|u\|)$ as $u \to 0$ in $C^1(\bar{\Omega})$, where $\| \, \|_\alpha$ denotes the norm in $C^\alpha(\bar{\Omega})$.

We may write (2.5) as

$$u = aKu + KFu \tag{2.7}$$

Since $\|KFu\| = o(\|u\|)$ as $u \to 0$ in $C^1(\bar{\Omega})$, the well known bifurcation results of Crandall and Rabinowitz [5] and Rabinowitz [10] can be applied to (2.7). Since $a = \lambda_1[f(0, v(0))]$ is a simple characteristic value of K, bifurcation occurs at this value of a and in a neighbourhood of the bifurcation point all non-trivial solutions lie on a continuous curve in $R \times C^1(\bar{\Omega})$ of the form $\{(a(\alpha), \psi(\alpha)): -\varepsilon \leqslant \alpha \leqslant \varepsilon\}$, where $a(0) = \lambda_1[f(0, v(0))]$ and $\psi(\alpha) =$

$\alpha\psi_1$ + terms of higher order in α. Thus for α sufficiently small and positive the corresponding non-trivial solutions lie in the cone

$$P = \left\{ u \in C^1(\bar{\Omega}) \colon u(x) > 0 \text{ for } x \in \Omega; \frac{\partial u}{\partial n}(x) < 0 \text{ for } x \in \partial\Omega \right\}.$$

Moreover, there exists a connected set of non-trivial solutions of (2.7) denoted by S such that either S joins $(\lambda_1[f(0, v(0))], 0)$ to ∞ in $R \times C^1(\bar{\Omega})$ or S joins $(\lambda_1[f(0, v(0))], 0)$ to $(b, 0)$, where b is some other characteristic value of K. In addition, S has a connected subset $S^+ \subset S - \{(a(\alpha), \psi(\alpha)) \colon -\varepsilon \leqslant \alpha < 0\}$ such that S^+ also satisfies one of the above alternatives. Clearly solutions (a, u) in S^+ sufficiently close to the bifurcation point lie in the cone $R \times P$. In fact more can be proved.

THEOREM 2.4. *The connected set of solutions S^+ is contained in $R \times P$ and joins $(\lambda_1[f(0, v(0))], 0)$ to ∞ in $R \times C^1(\bar{\Omega})$.*

Proof. Suppose that S^+ is not contained in $R \times P$; we shall obtain a contradiction. Then there exists $(a_0, u_0) \in S^+ \cap (R \times \partial P)$ such that $(a_0, u_0) \neq (\lambda_1[f(0, v(0))], 0)$ and (a_0, u_0) is the limit of a sequence $\{(a_n, u_n)\}$ contained in $S^+ \cap (R \times P)$. Choose $M > 0$ such that $a_0 + f(u_0(x), v(u_0)(x)) - f(0, v(0)(x)) + M > 0$ and $M - f(0, v(0)(x)) > 0$ for all $x \in \Omega$. Then as u_0 satisfies

$$(L + M)\, u_0 = (a_0 + f(u_0, v(u_0)) - f(0, v(0)) + M)\, u_0 \qquad \text{for} \quad x \in \Omega$$

we have

$$(L + M)\, u_0(x) \geqslant 0 \qquad \text{for} \quad x \in \Omega. \tag{2.8}$$

Since $u_0 \in \partial P$, either u has an interior zero in Ω or $\partial u_0/\partial n$ has a zero at a point of $\partial\Omega$. Hence it follows from (2.8) and the strong maximum principle that $u_0 \equiv 0$. Thus $(a_0, 0)$ is a bifurcation point.

We now show that $a_0 = \lambda_1[f(0, v(0))]$. Let $v_n = u_n/\|u_n\|$. Then

$$v_n = a_n K v_n + KF(u_n)/\|u_n\|. \tag{2.9}$$

Since $K \colon C^1(\bar{\Omega}) \to C^1(\bar{\Omega})$ is compact, there exists a subsequence of $\{v_n\}$ (which for convenience we again denote by $\{v_n\}$) such that $\{Kv_n\}$ converges in $C^1(\bar{\Omega})$. Since $\lim_{n \to \infty} KF(u_n)/\|u_n\| = 0$ in $C^1(\bar{\Omega})$, it follows that the subsequence $\{v_n\}$ itself converges in $C^1(\bar{\Omega})$ to v_0 say. Letting $n \to \infty$ in (2.9), we obtain

$$v_0 = a_0 K v_0.$$

Since $u_n \geqslant 0$ for all n, $v_0 \geqslant 0$; since $\|v_n\| = 1$ for all n, $v_0 \not\equiv 0$. Hence a_0 is a characteristic value of K corresponding to a non-negative eigenfunction and so $a_0 = \lambda_1[f(0, v(0))]$. This is a contradiction and so S^+ is contained in $R \times P$.

An argument similar to that used in the above paragraph shows that S^+ does not contain any points of the form $(a, 0)$, where a is a characteristic value of K other than $\lambda_1[f(0, v(0))]$. Hence it follows that S^+ joins $(\lambda_1[f(0, v(0))], 0)$ to ∞ in $R \times C^1(\bar{\Omega})$.

3. Multiple Solutions

We now make more detailed assumptions about the nature of the interaction between the two populations and deduce existence results in all possible cases of interactions. Throughout we shall assume that f and g satisfy the hypotheses (1.2), (1.3) and (1.4).

(a) *Predator–Prey Systems*

Suppose that v represents a predator population which preys on the population represented by u. Then an increase in the u population increases v's food supply and so would lead to an increase in the v population, whereas in increase in the v population increases predation and so would lead to a decrease in the u population. Hence it is natural to assume that

$$\frac{\partial f}{\partial v}(u, v) < 0 \text{ and } \frac{\partial g}{\partial u}(u, v) > 0 \qquad \text{for all} \quad u, v \geqslant 0. \tag{3.1}$$

On the other hand, if u represents the predator and v represents the prey, it is natural to assume that

$$\frac{\partial f}{\partial v}(u, v) > 0 \text{ and } \frac{\partial g}{\partial u}(u, v) < 0 \qquad \text{for all} \quad u, v \geqslant 0. \tag{3.2}$$

The next theorem gives a reasonable description of the steady state solutions of (1.5) for the case of a predator–prey system.

THEOREM 3.1. *Suppose that f and g satisfy either* (3.1) *or* (3.2).

(i) *Let $a < \lambda_1[f(0, v(0))]$. Then* (1.5) *has the unique non-negative solution $u = 0$, $v = v(0)$.*

(ii) *Let $a > \lambda_1[f(0, v(0))]$. Then* (1.5) *has at least one non-trivial non-negative solution.*

Proof. (a) Suppose that f and g satisfy (3.1).

(i) Suppose $a < \lambda_1[f(0, v(0))]$. Let (u, v) be any non-negative solution of (1.5). Then u satisfies (2.5) and multiplying (2.5) by u and integrating give

$$\int_\Omega Lu \cdot u\, dx = a\int_\Omega u^2\, dx + \int_\Omega [f(u, v(u)) - f(0, v(0))]\, u^2\, dx. \quad (3.3)$$

By the spectral theorem

$$\int_\Omega Lu \cdot u\, dx \geqslant \lambda_1[f(0, v(0))] \int_\Omega u^2\, dx.$$

Moreover, hypotheses (1.3), (3.1) and Theorem 2.2 show that $f(u, v(u)) - f(0, v(0)) \leqslant 0$. Hence it follows from (3.3) that

$$(\lambda_1\, [f(0, v(0))] - a) \int_\Omega u^2\, dx \leqslant 0$$

and so $u \equiv 0$. Therefore $u = 0$, $v = v(0)$ is the unique solution of (1.5).

(ii) We shall prove the result by showing that $\{a: (a, u) \in S^+\} = (\lambda_1[f(0, v(0))], \infty)$.

Suppose $(a, u) \in S^+$. Then, by (i), $a \geqslant \lambda_1[f(0, v(0))]$. We choose $M(a) > 0$ such that $a + f(M(a), 0) < 0$. Let $D = \{x \in \Omega: u(x) > M(a)\}$. Then, for all $x \in D$,

$$\begin{aligned} -d_1\, \Delta u(x) &= [a + f(u(x), v(x))]\, u(x) \\ &\leqslant [a + f(M(a), 0)]\, u(x) \leqslant 0. \end{aligned}$$

Since $u(x) = M(a)$ for all $x \in \partial D$, it follows from the maximum principle that $u(x) \leqslant M(a)$ for all $x \in D$. Hence $u(x) \leqslant M(a)$ for all $x \in \Omega$. If we choose $M_1(a) > 0$ such that $b + g(M(a), M_1(a)) < 0$ and $M_1(a) > \phi(x)$ for $x \in \partial\Omega$, it follows as in the proof of Theorem 2.1 that $0 \leqslant v(u)(x) \leqslant M_1(a)$ for $x \in \Omega$. Hence the right hand side of Eq. (2.4) is bounded in $C(\bar{\Omega})$ with the bound being independent of u and so standard bootstrapping arguments show that there exists $M_2(a) > 0$ such that $\|u\| < M_2(a)$, where as usual $\|\ \|$ denotes the $C^1(\bar{\Omega})$ norm.

Thus, if $\{a: (a, u) \in S^+\}$ were bounded, S^+ would be bounded in $R \times C^1(\bar{\Omega})$ which is impossible. Hence $\{a: (a, u) \in S^+\}$ is unbounded and so, since this set is also connected, it must equal $(\lambda_1[f(0, v(0))], \infty)$. Therefore, if $a > \lambda_1[f(0, v(0))]$, there exists u such that $(a, u) \in S^+$, i.e., (1.5) has a non-trivial non-negative solution.

(b) Suppose now that f and g satisfy (3.2).

(i) Since we again have $f(u, v(u)) - f(0, v(0)) \leqslant 0$, the result can be proved by using the same argument as above.

(ii) As above we establish the result by showing that $\{a: (a, u) \in S^+\} = (\lambda_1[f(0, v(0))], \infty)$.

Let $(a, u) \in S^+$. We can choose $K > 0$ such that $b + g(0, K) < 0$ and $K > \phi(x)$ for $x \in \partial\Omega$. Then it follows that $0 \leqslant v(u) \leqslant K$. We can now choose $K_1(a) > 0$ such that $a + f(K_1(a), K) < 0$ and then, by an argument similar to that used above, it follows that $0 \leqslant u \leqslant K_1(a)$. Thus, as above, it follows that $\{a: (a, u) \in S^+\} = (\lambda_1[f(0, v(0))], \infty)$ and the proof is complete.

It is interesting to note that although hypotheses (3.1) and (3.2) give rise to the same mathematical theorem there is a difference in the biological interpretation in the two cases. Suppose the quantities d_1, d_2, ϕ and b are fixed and consider the effect on the system of the birth rate a. When hypothesis (3.1) holds, i.e., when u is the prey, we have that $f(0, v(0)) \leqslant 0$ and so $\lambda_1[f(0, v(0))] \geqslant \lambda_1(0) > 0$. Hence in this case in order for there to be a steady state in which the u and v populations co-exist we must have that the birth rate of u is greater than a given positive number. When hypothesis (3.2) holds, i.e., when u is the predator, we have that $f(0, v(0)) \geqslant 0$ and so the sign of $\lambda_1[f(0, v(0))]$ is unclear. If ϕ and b are small, $v(0)$ and $f(0, v(0))$ will be small and so we will again have $\lambda_1[f(0, v(0))] > 0$ and the biological interpretation is the same as above. If, however, the prey v is supplied more generously to the system, i.e., if ϕ or b is large, $v(0)$ and $f(0, v(0))$ will be large and so we may have $\lambda_1[f(0, v(0))] < 0$. In this case the theorem tells us that there is a steady state in which the u and v populations co-exist if u has a net positive birth rate or a sufficiently small net mortality rate.

(b) *Competing Populations*

We now consider the case where u and v are competing populations. Thus we shall assume throughout this section that

$$\frac{\partial f}{\partial v}(u, v) < 0 \text{ and } \frac{\partial g}{\partial u}(u, v) < 0 \qquad \text{for} \quad u, v \geqslant 0. \tag{3.4}$$

The results of Section 2 again guarantee bifurcation from the point $(\lambda_1[f(0, v(0))], 0)$. However, as the next theorem shows, our description of the parameter values for which non-trivial steady state solutions exist is less precise than that in the predator–prey case. Note that because of hypotheses (3.4) $f(0, v(0)) \leqslant 0$ and so $\lambda_1[f(0, v(0))] \geqslant \lambda_1(0)$.

THEOREM 3.2. (i) *Let $a < \lambda_1(0)$. Then* (1.5) *has the unique non-negative solution $u = 0$, $v = v(0)$.*

(ii) *Let $a > \lambda_1[f(0, v(0))]$. Then* (1.5) *has at least one non-trivial non-negative solution.*

Proof. (i) Suppose $a < \lambda_1(0)$ and (a, u) satisfies (2.4). Multiplication of (2.4) by u and integration give

$$-d_1 \int_\Omega \Delta u \cdot u \, dx = a \int_\Omega u^2 \, dx + \int_\Omega f(u, v(u)) \, u^2 \, dx$$

and so

$$(\lambda_1(0) - a) \int_\Omega u^2 \, dx \leqslant \int_\Omega f(u, v(u)) \, u^2 \, dx \leqslant 0.$$

Hence $u \equiv 0$ and this completes the proof.

(ii) Suppose $(a, u) \in S^+$. By (i), $a \geqslant \lambda_1(0)$. We shall show that there exists a constant $M(a) > 0$ such that $\|u\| < M(a)$. Using an argument similar to that of Theorem 3.1, the existence of this bound shows that $\{a : (a, u) \in S^+\}$ is a semi-infinite interval bounded below which contains $\lambda_1[f(0, v(0))]$ and so the required result follows.

We choose $M_1(a) > 0$ so that $a + f(M_1(a), 0) < 0$ and $M_2 > 0$ so that $b + g(0, M_2) < 0$ and $M_2 > \phi(x)$ for $x \in \partial\Omega$. Arguments similar to those we have used before show that $0 \leqslant u \leqslant M_1(a)$ and $0 \leqslant v(u) \leqslant M_2$. It now follows that the right hand side of (2.4) is bounded in $C(\bar{\Omega})$, the bound depending only on a and not on u, and so standard bootstrapping arguments prove the existence of a constant $M(a) > 0$ such that $\|u\| < M(a)$. Thus the proof is complete.

The biological interpretation of the above theorem is that in the case of competing species there are steady state solutions in which the u and v populations co-exist provided the birth rate of the population is sufficiently large.

(c) *Co-operating Populations*

Finally we consider the case where the presence of the u population encourages the growth of the v population and vice versa. We assume that

$$\frac{\partial f}{\partial v}(u, v) > 0 \text{ and } \frac{\partial g}{\partial u}(u, v) > 0 \qquad \text{for} \quad u, v \geqslant 0. \tag{3.5}$$

Again Theorem 2.4 guarantees the existence of a family of non-negative solutions bifurcating from $(\lambda_1[f(0, v(0))], 0)$. It is intuitively obvious that in this case the size of possible steady state solutions can no longer be bounded in terms of the birth rates of u and v, i.e., since the populations co-operate, very large steady state solutions seem possible even when the birth rates are small. In order to obtain results similar to those obtained for the other types of systems we must limit the extent of the co-operation between u and v. Hence we make the following additional assumption on g:

$$\text{there exists } M > 0 \text{ such that } b + g(u, M) < 0 \quad \text{for all } u \geqslant 0. \tag{3.6}$$

For example, $g(u,v) = u/(1+u) - v$ satisfies (3.6). In the next lemma we use hypothesis (3.6) in order to obtain an a priori bound on $v(u)$.

LEMMA 3.3. *There exists $M_0 > 0$ such that $0 \leqslant v(u) \leqslant M_0$ for all $u \in C^1(\bar{\Omega})$.*

Proof. Choose M_0 so that $M_0 > M$ (where M is as in (3.6)) and $M_0 > \phi(x)$ for $x \in \partial\Omega$. Then the same arguments as those used in Theorem 3.1 show that $0 \leqslant v(u) \leqslant M_0$.

We can now give some description of the family of steady state solutions. Note that, as $v(0) \leqslant M_0$, $f(0, M_0) \geqslant f(0, v(0)) \geqslant 0$ and so $\lambda_1 [f(0, M_0)] \leqslant \lambda_1 [f(0, v(0))]$.

THEOREM 3.4. (i) *Let $a < \lambda_1 [f(0, M_0)]$. Then* (1.5) *has the unique non-negative solution $u = 0$, $v = v(0)$.*

(ii) *Let $a > \lambda_1 [f(0, v(0))]$. Then* (1.5) *has at least one non-trivial non-negative solution.*

Proof. (i) Suppose $a < \lambda_1 [f(0, M_0)]$ and (a, u) is a solution of (2.4). Then

$$-d_1 \Delta u - f(0, M_0) u = au + [f(u, v(u)) - f(0, M_0)] u$$

and so

$$\int_\Omega [-d_1 \Delta u - f(0, M_0) u] u \, dx = a \int u^2 \, dx + \int_\Omega [f(u, v(u)) - f(0, M_0)] u^2 \, dx.$$

Since $f(u, v(u)) - f(0, M_0) \leqslant 0$, it follows that

$$(\lambda_1 [f(0, M_0)] - a) \int_\Omega u^2 \, dx \leqslant 0$$

and so $u \equiv 0$. This completes the proof of (i).

(ii) Suppose $(a, u) \in S^+$. Using Lemma 3.3 and arguments similar to those of Theorem 3.1, it can be shown that there exists $M(a) > 0$ such that $\|u\| < M(a)$ and the result now follows by arguments similar to those used in the previous theorems.

A theorem similar to Theorem 3.4 can be obtained if hypothesis (3.6) on g is replaced by the following hypothesis on f:

$$\begin{aligned} &\text{for every } a \geqslant 0 \text{ there exists } M(a) > 0 \text{ such that} \\ &a + f(M(a), v) < 0 \text{ for all } v \geqslant 0. \end{aligned} \tag{3.7}$$

Since $f(0, M_0), f(0, v(0)) > 0$, the signs of $\lambda_1[f(0, M_0)]$ and $\lambda_1[f(0, v(0))]$ are uncertain. Hence the biological interpretation is similar to that in the case where u represents a predator and v represents a prey. In particular, provided that v is supplied generously to the system, i.e., b or ϕ is large, there will be steady state solutions in which u and v co-exist even when u has a (sufficiently small) net mortality rate.

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